## Uncertainties modelling CH4 emissions from Northern wetlands in glacial climates: the role of vegetation and microbial community parameters

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Climate of the Past

# Uncertainties in modelling $CH_4$ emissions from northern wetlands in glacial climates: the role of vegetation parameters

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**Abstract.** Marine Isotope Stage 3 (MIS 3) interstadials are marked by a sharp increase in the atmospheric methane ($CH_4$) concentration, as recorded in ice cores. Wetlands are assumed to be the major source of this $CH_4$, although several other hypotheses have been advanced. Modelling of $CH_4$ emissions is crucial to quantify $CH_4$ sources for past climates.

Vegetation effects are generally highly generalized in modelling past and present-day $CH_4$ fluxes, but should not be neglected. Plants strongly affect the soil-atmosphere exchange of $CH_4$ and the net primary production of the vegetation supplies organic matter as substrate for methanogens. For modelling past $CH_4$ fluxes from northern wetlands, assumptions on vegetation are highly relevant since paleobotanical data indicate large differences in Last Glacial (LG) wetland vegetation composition as compared to modern wetland vegetation. Besides more cold-adapted vegetation, *Sphagnum* mosses appear to be much less dominant during large parts of the LG than at present, which particularly affects $CH_4$ oxidation and transport. To evaluate the effect of vegetation parameters, we used the PEATLAND-VU wetland $CO_2/CH_4$ model to simulate emissions from wetlands in continental Europe during LG and modern climates.

We tested the effect of parameters influencing oxidation during plant transport ($f_{ox}$), vegetation net primary production (NPP, parameter symbol $P_{max}$), plant transport rate ($V_{transp}$), maximum rooting depth ($Z_{root}$) and root exudation rate ($f_{ex}$). Our model results show that modelled $CH_4$ fluxes are sensitive to $f_{ox}$ and $Z_{root}$ in particular. The effects of $P_{max}$, $V_{transp}$ and $f_{ex}$ are of lesser relevance. Interactions with water table modelling are significant for $V_{transp}$.

We conducted experiments with different wetland vegetation types for Marine Isotope Stage 3 (MIS 3) stadial and interstadial climates and the present-day climate, by coupling PEATLAND-VU to high resolution climate model simulations for Europe. Experiments assuming dominance of one vegetation type (*Sphagnum* vs. *Carex* vs. *Shrubs*) show that *Carex*-dominated vegetation can increase $CH_4$ emissions by 50 % to 78 % over *Sphagnum*-dominated vegetation depending on the modelled climate, while for shrubs this increase ranges from 42 % to 72 %. Consequently, during the LG northern wetlands may have had $CH_4$ emissions similar to their present-day counterparts, despite a colder climate. Changes in dominant wetland vegetation, therefore, may drive changes in wetland $CH_4$ fluxes, in the past as well as in the future.

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## 1 Introduction

Interstadials during the last glacial and previous glacials show a conspicuous increase in the atmospheric $CH_4$ concentration, which is recorded in ice cores (Brook et al., 2000; EPICA, 2004). Several studies have addressed $CH_4$ fluxes from wetlands during past glacial climate warming phases to explain the origin of these elevated $CH_4$ concentrations (van Huissteden, 2004; Valdes et al., 2005; Kaplan et al., 2006; Harder et al., 2007). Such warming phases may also serve as an analogue for the effects of present warming on northern wetlands (Berrittella and van Huissteden, 2009). However, a complicating factor is the effect of vegetation on $CH_4$ emissions. Vegetation affects $CH_4$ fluxes from wetlands, modifying both the transfer of labile organic carbon into anoxic soils and the transfer of $CH_4$ from soil to the atmosphere. In large scale $CH_4$ emission models, this is often overlooked and it leads to simplistic descriptions of the wetland $CH_4$ flux

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dynamics (Berrittella and van Huissteden, 2009; van Huissteden et al., 2009; Petrescu et al., 2010).

Glacial-interglacial and stadial-interstadial climate changes may have induced shifts in vegetation patterns or complete biomes. Also, vegetation and ecosystems which have no analogue today may have existed. Global vegetation model simulations involving past climates might be used, although these have yielded results significantly different from paleobotanical data (Huntley et al., 2003). An example of non-analogue vegetation is the abundance of *Sphagnum* mosses in present-day and glacial wetlands. In MIS 3 and 2 peaty deposits in Europe, *Sphagnum* mosses are practically lacking (Behre, 1989; Ran, 1990; Huntley et al., 2003). In this respect, wetland flora during most of the last glacial differed markedly from modern, often *Sphagnum*-rich peatlands and tundra vegetation. The same holds for the last glacial environments in Siberia (e.g. Guthrie, 1990; Walker et al., 2003; Zazula et al., 2003; Zimov, 2005).

Models commonly include two groups of processes that are related to vegetation. The first group refers to production of labile organic compounds from gross primary production (GPP), used by methanogens in the anaerobic soil zone. The second group of processes is related to the transport of $CH_4$ to the atmosphere via plant stems and leaves (Walter and Heimann, 2000). The latter processes may be influential, but their parameterization is complicated as all parameters tend to be difficult to measure (e.g. Verville et al., 1998; Joabsson and Christensen, 2001).

Differences in vegetation effectively influence $CH_4$ fluxes as proved by King and Reeburgh (2002), documenting the relation between $CH_4$ and net primary production (NPP) in tundra vegetation. Verville et al. (1998) and Busch and Lösch (1999) have also shown the importance of plant transport of $CH_4$ through their aerenchymous tissues (tissues containing channels for gas exchange) and the differences between vegetation types. During such transport oxidation of $CH_4$ may also occur. As shown by Raghoebarsingh et al. (2005), symbiosis between *Sphagnum spp.* and methanotrophic bacteria (methanotrophs) allows within-plant oxidation of $CH_4$ even when plants are submerged. Considerable spatial variations in fluxes related to vegetation differences have been found in northern wetlands (e.g. Turetsky et al., 2002; Wagner et al., 2003; van Huissteden et al., 2005; van der Molen et al., 2007; Parmentier et al., 2011a,b). Such variations have been ascribed to differences in NPP, plant transport and oxidation of $CH_4$ and can be reproduced by plot-scale models, if the vegetation parameters of the model are correctly specified (Petrescu et al., 2008; van Huissteden et al., 2009; Parmentier et al., 2011a). Changes in peatland vegetation (area fraction of Carex and Sphagnum vegetation and pools) also may influence future northern wetland $CH_4$ emissions (Frenzel and Karofeld, 2000; Strack et al., 2006).

For global scale model simulations of $CH_4$ fluxes, the relevance of these vegetation-related processes is difficult to determine, although wetlands generally consist of mosaics of plants which may be constant in wide geographic areas (Charman, 2002). Therefore, it could be justified to lump vegetation effects all together. A precise characterization of vegetation conditions generally remains out of scope for global scale simulations, even though regional attempts have already been made using remote sensing data (Kutzbach et al., 2004; Schaepman-Strub et al., 2009).

During MIS 3, wetlands were largely dominated by *Cyperaceae spp.* (Ran, 1990) with the occurrence of bryophytes other than *Sphagnum*. The cause may have been the ubiquitous presence of soils with generally high pH value caused by frequent cryoturbation processes, erosion/sedimentation of fresh, relatively unweathered sediment (e.g. Ran, 1990) and deposition of generally calcareous loess (van Huissteden, 1990; Walker and Everett, 1991). Also low atmospheric $CO_2$ concentrations may have decreased the expansion of *Sphagnum* mosses (Heijmans et al., 2005).

The quality of organic matter in the substrate influences microbial metabolism and can act as a major limitation factor in their growth rates (Wagner et al., 2005). Thus, vegetation characteristics affecting the transfer of photosynthesis products to labile organic carbon in the soil may also have a large effect on $CH_4$ fluxes (King and Reeburgh, 2002), e.g. root exudation and root distribution.

We hypothesize that large differences in vegetation between modern and past northern lowlands may have influenced past northern wetland fluxes, and this article explores the effect of vegetation parameters on a large scale model of $CH_4$ fluxes for the LG and modern climate. Our modelling experiments on past glacial climates are fully described in Berrittella and van Huissteden (2009), where PEATLAND-VU model output was validated with present-day fluxes from natural wetlands by using the modern climate control experiment of the paleoclimate simulations, to drive the $CH_4$ emission model. That study also explored the effects of model complexity and water table modeling. The values obtained in the experiments are annual emissions from the European region displayed in Fig. 1, respectively for Modern and LG MIS 3 warm/interstadial and cold/stadial climates.

## 2 Effects of plants on $CH_4$ fluxes

There are three main pathways for transport of $CH_4$ from the soil to the atmosphere (e.g. Hutchin et al., 1996; Chanton, 2005):

1. Molecular diffusion, which is dependent on soil characteristics, such as porosity and permeability of the soil. During diffusion, $CH_4$ may be consumed by methanotrophic bacteria in oxygenated soil zones.

2. Ebullition, effective when a threshold $CH_4$ concentration is reached in water saturated soil, so that $CH_4$ bubbles can form and rise to the soil surface.

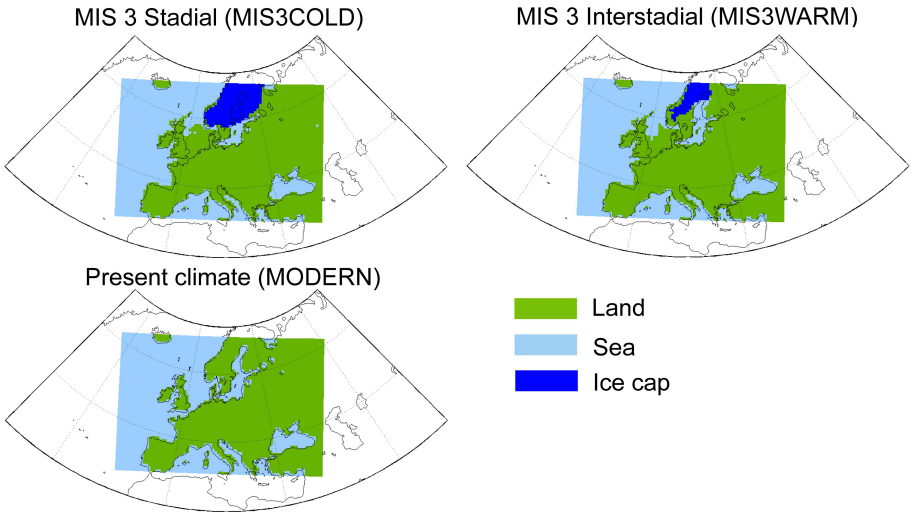


**Fig. 1.** Land, sea and glacial ice distribution for the MIS3 stadial (MIS3COLD), interstadial (MIS3WARM) and present-day control (MODERN) climate model experiments of the Stage 3 project (see Barron and Pollard, 2002 for a more extensive description of the STAGE3 climate model runs).

3. Plant transport from the root zone through aerenchymous tissue of plants. This may provide a fast shortcut to bypass methanotrophic bacteria in oxygenated topsoil. On the other hand, $CH_4$ may be exposed to oxidation in the root zone and during transport in the plant as well.

Couwenberg (2009) ranks the importance of each pathway in percentage terms, allocating 2 % of the total fluxes to molecular diffusion, while ebullition is held responsible for 48 % and plants account for the remaining 50 %.

As the vegetation density increases, so does the proportion of the fluxes released to the atmosphere through plants; conversely the value for ebullition-related emissions decreases (Bazhin, 2003). Otherwise ebullition can be very efficient in completely water-saturated soils (Lai, 2009), due to the low solubility of $CH_4$ in water and the rapid transfer of bubbles (Boone, 2000) and can be enhanced by a decrease in atmospheric or hydrostatic pressure (Tokida et al., 2007; Strack et al., 2005).

Oxidation of $CH_4$ is mainly associated with the root system of wetland plants, although it also occurs inside plants and at their surface. Methanotrophs occupy oxic zones at the root-soil interface (van der Nat and Middelburg, 1998; Popp et al., 2000; Smialek et al., 2006; Hornibrook, 2009) where oxygen is supplied by plant transport. Plants can actively drive gas exchange and therefore, this gas exchange rate is partly dependent on metabolism (Walter and Heimann, 2000). Ström et al. (2005) demonstrated considerable differences in rhizosphere $CH_4$ oxidation between wetland plants; *Juncus effusus* and *Eriophorum vaginatum* showed high oxidation (>90 %) compared to *Carex rostrata* (20–40 %). The high oxidation in the root system of Juncus effusus is attributed to an efficient oxygen supply to the roots (Smialek et al., 2006). Popp et al. (2000) found lower oxidation for *Carex* (0–34 %). However, the oxidation in the root system is difficult to determine, and Popp et al. (2000) note considerable differences between methods. According to an experiment by Berestovskaya et al. (2005), $CH_4$ oxidation was found to occur in bog water, in green parts of peat moss and in all the soil horizons investigated, while its production was recorded in peat horizons, in clay with plant roots, and in peaty moss areas. Gas consumption by $CH_4$-oxidizing bacteria in the vegetation is also supported by data from the incubation of marsh plants with up to 88 % $CH_4$ depletion (Calhoun and King, 1997). Heilmann and Carlton (2001) demonstrate oxidation at the surfaces of submerged plants.

Raghoebarsingh et al. (2005) have described a symbiosis of methanotrophs with *Sphagnum* species. The methanotrophs live inside the plant between leaf cells and convert $CH_4$ to $CO_2$, providing the plant with $CO_2$ for photosynthesis. Kip et al. (2010) have demonstrated the widespread occurrence of this symbiosis; high oxidation rates were measured in particular from samples derived from northeast Siberian tundra (Parmentier et al., 2011a), collected by the first author of this paper. *Sphagnum* species are able to decrease $CH_4$ fluxes from the soil by 40 % to 90 % of what would otherwise have been emitted into the atmosphere (Kip et al., 2010; Parmentier et al., 2011a).

For global scale modeling of $CH_4$ emissions, it would be useful to extend the widely used concept of Plant Functional Type (PFT) with these fundamental aspects of the carbon cycle. Wania et al. (2010) introduced two PFT's specifically for wetland methane modeling (flood-tolerant $C_3$ graminoids and Sphagnum mosses). Similarly, we grouped wetland plants according to their $CH_4$ transport

**Table 1.** Wetland plant functional types and their main characteristics as used in the model experiments.

| Wetland vegetation type | Description | Transport | Oxidation | Spatial distribution |
|---|---|---|---|---|
| *Carex* type | Hollow stems, Cyperaceae, Gramineae, often dominated by Carex | Rapid to intermediate | Usually low, in rhizosphere | Riparian, fens, lawns in ombotrophic bogs |
| *Sphagnum* type | Dominated by *Spahgnum* | Minimal | High inside plant | Ombrotrophic bogs, hummocks and pools |
| *Shrubs* resistant to wet conditions | *Salix* and other species | Intermediate | Intermediate ombrotrophic, tundra | Riparian, |

and oxidation capacity, suited to model $CH_4$ emissions. The following two factors were taken into account in this classification:

1. The oxidation of $CH_4$ during plant transport. A major role is played by the metabolism of the plant, whether or not there is a bacterial community able to decompose $CH_4$ and whether it is supplied with oxygen.

2. The transport rate. For most vascular wetland plants, aerenchymous tissue in roots and stems allows passive or active transport of gases from the atmosphere to the root system, to exchange reduced soil gases for oxygen (Verville et al., 1998; Joabsson and Christensen, 2001; Oquist et al., 2002).

Species displaying any combination of low oxidation and fast transport will give $CH_4$ fluxes higher than those species with high oxidation and low transport. Therefore, transport rate itself cannot be sufficient to define the effectiveness of a plant relative to $CH_4$ emissions. For usage in our model experiments outlined below, we distinguish three main classes of wetland vegetation with respect to their functionality in $CH_4$ soil atmosphere transport (Table 1):

1. Graminoid vegetation dominated by *Cyperaceae* and *Gramineae*. As indicated above, oxidation can vary between different species from low to high (e.g. *Carex sp.* vs. *Juncus*). However, this vegetation is usually dominated by *Carex* species in northern wetlands, and in paleobotanical sections, abundant remains of *Carex* are usually found. Therefore, we denote it here as *Carex*-type vegetation and assume domination by *Carex* species. Its main characteristics are the dominance of aerenchymous gas transport through hollow roots and stems and low oxidation rate. This results in high $CH_4$ emissions rates in wetlands (e.g. van Huissteden et al., 2005, 2009; Parmentier et al., 2011a,b). Based on the inter-species variability in the rhizosphere oxidation rate, more classes could be distinguished with intermediate or high oxidation (e.g. *Juncus*), but the paleobotanical significance of these distinctions would be speculative.

2. Vegetation dominated by *Sphagnum* mosses, non vascular plants without a root system, and a well documented symbiosis with methanotrophic bacteria (Raghoebarsingh et al., 2005). Therefore, $CH_4$ emissions from areas dominated by these mosses are usually smaller than others.

3. Shrubs, such as *Salix ssp.*, have been also taken into account, because they may be abundant in some wetland types. The few data that exist on $CH_4$ oxidation and transport properties suggest intermediate behavior, showing neither rapid rates of transport nor high oxidation potential. For instance, the oxidation in *Salix nigra* was moderated by decreased root density in wet conditions (Smialek et al., 2006). Generally these plants occupy drier sites in northern wetlands and are adapted to occasional flooding only.

These classes are not meant to represent a full classification of wetland PFT's but to represent classification end members of wetland vegetation with respect to vegetation-mediated $CH_4$ emission, designed on behalf of our model experiments. Other species' groups from drier habitats have not been included here as they cannot affect $CH_4$ emissions (Holzapfel-Pschorn et al., 1986; Laanbroek, 2009). Other vegetation characteristics, for instance the leaf area index (LAI), have no direct effect on $CH_4$ fluxes, although high primary production enhances substrate availability for methanogens.

## 3 Modelling experiments

### 3.1 The PEATLAND-VU model

PEATLAND-VU is a process-based model, for $CO_2$ and $CH_4$ emission from wetland soils under various climate scenarios. It consists of four sub-models: a soil physics submodel to calculate temperature (including soil freezing) and water saturation of the soil layers, a $CO_2$ sub-model, a $CH_4$

sub-model, and an organic production sub-model (Walter and Heimann, 2000; van Huissteden et al., 2006). The model includes several labile and refractory organic matter reservoirs (peat substrate, manure, roots and litter, root exudates and refractory humic matter).

In the $CH_4$ sub-model, gas production below the water table linearly depends on labile organic carbon concentration, multiplied by a production rate factor $R_0$. We assumed a small contribution from peat to $CH_4$ formation using a rate constant $R_{0,\mathrm{peat}}$ of $0.01 \times$ the $R_0$ for labile organic matter in the model. The labile carbon pool is produced by the transfer of net primary production (NPP) into root exudates and plant litter. This depends on linear conversion factors for root-shoot and root-exudate allocation of NPP ($f_{\mathrm{shoots}}$, $f_{\mathrm{ex}}$), and the vertical root density distribution (exponential, determined by maximum rooting depth $Z_{\mathrm{roots}}$). NPP depends on a maximum daily NPP $P_{\mathrm{max}}$. Above the water table, $CH_4$ is oxidized by methanotrophs, which depends on $CH_4$ concentration and is modelled using a Michaelis-Menten relation (Walter and Heimann, 2000). Soil-atmosphere transport includes diffusion, ebullition and transport by plants. Ebullition depends on a soil $CH_4$ concentration threshold. Plant transport depends on soil $CH_4$ concentration, root density, plant growth rate, and a vegetation-dependent factor, $V_{\mathrm{transp}}$. During transport, part of the $CH_4$ may be oxidized, which is modelled using a plant oxidation factor $f_{\mathrm{ox}}$. This includes all plant-related oxidation (within the rhizosphere, in plant tissue and at the plant surface).

To summarize, vegetation processes influencing $CH_4$ fluxes in this model are: maximum NPP, a factor for all $CH_4$ that is oxidized during plant transport, partitioning of NPP among shoot and root production and the fraction of NPP transferred into below-ground labile organic carbon (the main substrate for methanogens), and a factor quantifying plant transport rate (van Huissteden et al., 2006; Walter and Heimann, 2000). Several of these parameters are poorly quantified, yet strongly determine model results (van Huissteden et al., 2009). These parameters are displayed in Table 2.

### 3.2 Climate model input to PEATLAND-VU

These experiments link the PEATLAND-VU model to the climate model experiments for the "STAGE 3" project on climate and landscape of Middle Weichselian Europe (van Andel, 2002; Barron and Pollard, 2002). They simulate the LG stadial and interstadial climates, together with a modern climate control experiment, at a high spatial resolution over Europe. The simulations focus on the climate of the MIS 3 stadials and interstadials. The climate model experiments were coupled interactively to the BIOME 3.5 global vegetation model.

PEATLAND-VU is linked to the climate model by the output of monthly-averaged near-surface air temperature, precipitation and evaporation. These drive PEATLAND-VU and a water table model based on Cao et al. (1996). The PEATLAND-VU output is integrated over a topography-derived wetlands map which includes the areas that are exposed at the lower sea level stands of the LG (Berrittella and van Huissteden, 2009), denoted as "seafloor" below. We show the results separately for present-day land and exposed seafloor. This distinction of exposed seafloor fluxes is crucial, to separate the effects of changes in global topography from other climate- and vegetation-induced fluxes. For a complete description of the model input see Berrittella and van Huissteden (2009). We use here the climate simulations for stadial and interstadial conditions, representing a typical MIS 3 stadial and interstadial (MIS3COLD and MIS3WARM simulations respectively), and the present-day climate control experiment (MODERN hereafter). The MIS3WARM (interstadial) simulation matches paleoclimate data more closely than the other simulations of the STAGE 3 experiments; the MIS3COLD climate model experiment shows higher temperatures than several paleoclimate proxies indicate, e.g. the extent of permafrost (van Huissteden et al., 2003; Berrittella and van Huissteden, 2009). The mean annual air temperatures over the land area in the model domain for MIS3WARM, MIS3COLD and MODERN are respectively 2.6 °C, 2.2 °C, and 6.6 °C, mean January temperatures −8.1 °C, −8.5,°C, and 19.5 °C. MIS3WARM is distinctly wetter than MIS3COLD, with mean annual precipitation over the land area of 732 vs. 674 mm (MODERN: 972 mm). The domain with land, sea and land ice distribution is shown in Fig. 1. The land areas for the model domains of MIS3COLD, MIS3WARM and MODERN are $9.31 \times 10^6\,\mathrm{km}^2$, $9.76 \times 10^6\,\mathrm{km}^2$, and $9.29 \times 10^6\,\mathrm{km}^2$; the area for MIS3WARM is the largest because of a relatively wider area of exposed seafloor and a smaller ice cap.

### 3.3 Model runs

A number of model runs have been performed to test the sensitivity of vegetation-related parameters separately (Table 2): $CH_4$ oxidation during plant transport $f_{\mathrm{ox}}$; maximum NPP $P_{\mathrm{max}}$; plant transport rate factor $V_{\mathrm{transp}}$; root exudation factor $f_{\mathrm{ex}}$; maximum rooting depth $Z_{\mathrm{root}}$. These runs have been restricted to the MIS3WARM climate only, since only relative differences between the experiments are relevant here, rather than the climate itself.

The water table (WT) greatly influences the $CH_4$ emissions, which are usually decreasing nearly exponentially when WT drops below the soil surface (Moore and Knowles, 1989; Moore and Dalva, 1993; Roulet et al., 1992; van Huissteden et al., 2005). We used two approaches to model the WT: a simple, fixed WT in which the WT is assumed to be at the soil surface throughout the year (van Huissteden, 2004) (FIXEDWT hereafter) or a simulated WT based on the precipitation and temperature output of the climate model (Berrittella and van Huissteden, 2009), cf. Cao et al. (1996) (MODELWT hereafter). The latter model results generally in a high spring and early summer water table and a decrease

**Table 2.** Vegetation and microbial population parameters used in PEATLAND-VU and the model experiments described below. If no units are given in column Units/range, the parameter is dimensionless. Column Symb: symbols used for the parameters; Column Ref: literature references; W-H is Walter and Heimann (2000); S is Shaver et al. (1996); H is van Huissteden et al. (2009).

| Parameter | Symb. | Description | Units/range | Ref. |
|---|---|---|---|---|
| Plant transport factor | $V_{transp}$ | Vegetation type factor for gas transport by plants | 0–15 | W-H |
| Oxidation fraction | $f_{ox}$ | Fraction of methane oxidized during transport by plants | 0–1 | W-H |
| Maximum net primary productivity | $P_{max}$ | Maximum daily NPP at optimum temperature conditions | $kg\,C\,m^{-2}\,day^{-1}$ 0.001–0.005 | S |
| Shoots factor | $f_{shoots}$ | Mass factor of NPP that consists of shoots, the remainder is root growth | 0.2–0.8 | S |
| Exudate factor | $f_{ex}$ | Mass factor of below-ground production turned into root exudates | 0.1–0.3 | H |
| Rooting depth | $Z_{root}$ | Maximum rooting depth | 0.2-0.5 | H |
| $CH_4$ production | $R_0$ | Production rate factor for $CH_4$ production from labile organic carbon | $\mu m\,h^{-1}$ | W-H |
| Temperature sensitivity $CH_4$ | $Q_{10}$ | $Q_{10}$ correction for temperature sensitivity of $CH_4$ production | 1.7–16 | W-H |

**Table 3.** Standard and PFT adapted values for vegetation parameters. The standard parameter values are used for runs when no vegetation distinction is made, as in Berrittella and van Huissteden (2009). Parameter symbols as in Table 2, Wetland PFT's as in Table 1.

| Wetland vegetation type | $R_0$ | $f_{ox}$ | $f_{shoot}$ | $Z_{root}$ | $V_{transp}$ |
|---|---|---|---|---|---|
| Standard value | 0.4 | 0.2 | 0.7 | 0.3 | 12 |
| *Carex* type | 0.4 | 0.2 | 0.5 | 0.4 | 12 |
| *Sphagnum* type | 0.2 | 0.9 | 0.8 | 0.1 | 4 |
| Shrubs | 0.3 | 0.1 | 0.6 | 0.4 | 10 |

of the water table in late summer, depending on the precipitation amount. Some model parameters are expected to interact with WT, since they are influenced by the (exponential) vertical root distribution: $V_{transp}$, $f_{ex}$. Therefore, we also tested these parameters with both approaches of water table modelling.

In the introduction, we mentioned how MIS3 wetland vegetation differed considerably from actual northern wetlands. To test the effects of observed differences between MIS 3 wetlands and present-day moss-rich tundra vegetation, we undertook experiments with the three dominant wetland vegetation types outlined in Table 1: *Carex*, *Sphagnum*, and shrubs (VEGETATION experiment). For each vegetation type, we used the parameter values as listed in Table 3. These parameters are based on the morphology of the plants, on the literature discussed above, and on previous model optimization (van Huissteden et al., 2009; Parmentier et al., 2011a). We assume a higher $CH_4$ production rate for the *Carex* type than for *Sphagnum* as indicated by sensitivity experiments by van Huissteden et al. (2009) and Parmentier et al. (2011a), probably reflecting better substrate quality. These sensitivity experiments also indicate value ranges for $f_{ox}$ and $V_{transp}$ for *Carex* and *Sphagnum*. The oxidation rate $f_{ox}$ is set to a low value for shrubs and *Carex*, and maximum for *Sphagnum*. The transport rate $V_{transp}$ and rooting depth $Z_{root}$ are set to a low value for *Sphagnum* vegetation and near maximum for *Carex* vegetation. In each case, we assume 100 % cover of each vegetation type. These experiments include the MIS3COLD, MIS3WARM and MODERN climate model runs. For these experiments, the NPP ($P_{max}$) values were derived from the BIOME 3.5 model. All fluxes in the experiments are calculated in Gigatons $CH_4$ per year ($GT\,yr^{-1}$) for the entire model domain shown in Fig. 1.

For all model runs, the soil profile is assumed uniform throughout the model domain and consists of an organic layer of 35 cm with 80 % organic matter overlying mineral soil based on typical MIS 3 wetland paleosoils (van Huissteden, 1990, 2004; Berrittella and van Huissteden, 2009). Van Huissteden et al. (2009) have shown that the model is relatively insensitive to soil parameters.

## 4 Results

Figure 2 shows the effect of oxidation of $CH_4$ during plant transport (the $f_{ox}$ parameter). Decreasing $f_{ox}$ , while keeping the other parameters constant, results in a linear decrease of

**Table 4.** Experimental results for parameter with a linear relation between parameter value and model output: oxidation fraction ($f_{ox}$), vegetation net primary production (NPP, parameter symbol $P_{max}$), and root exudation rate ($f_{ex}$). The numbers in the last three columns contain the modelled flux (Gt $CH_4$ $yr^{-1}$) at lower end of the modelled parameter range and the percentage increase (+) or decrease (−) at the higher end.

| Parameter | Symbol | Parameter range | Maximum model output change % | | |
|---|---|---|---|---|---|
| | | | Land | Seafloor | Total |
| Oxidation fraction | $f_{ox}$ | 0.2–0.9 | 5.10–60.3 % | 4.05–47.6 % | 1.05–57.7 % |
| Maximum net primary productivity | $P_{max}$ | 0.003–0.009 kg C $m^{-2}$ $day^{-1}$ | 4.77 + 9.7 % | 3.81 + 12.5 % | 0.97 + 10.3 % |
| Exudate factor MODELWT | $f_{ex}$ | 0.1–0.3 | 7.25 + 3.6 % | 6.18 + 3.6 % | 1.09 + 3.6 % |
| Exudate factor FIXEDWT | $f_{ex}$ | 0.1–0.3 | 6.35 + 4.7 % | 5.15 + 4.5 % | 1.29 + 4.6 % |

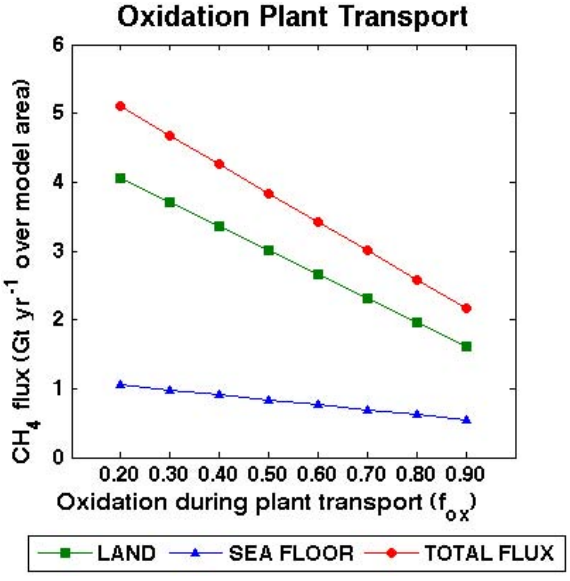


**Fig. 2.** Increasing the oxidation parameter ($f_{ox}$) values results in a strong decrease of the $CH_4$ emissions for the model domain. The decrease is linearly related to $f_{ox}$.

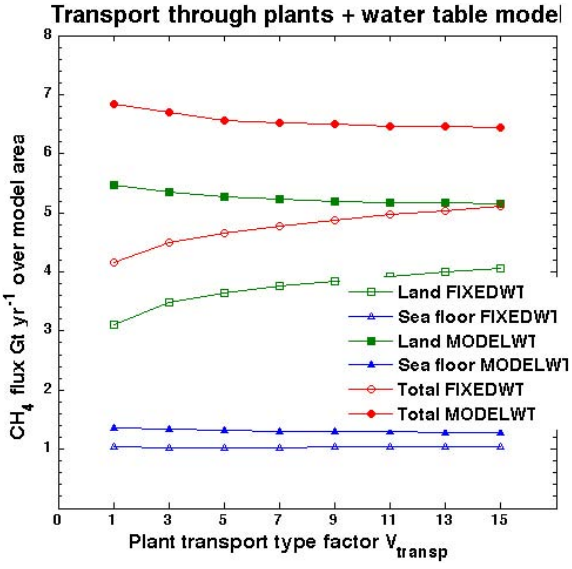


**Fig. 3.** The effects of plant transport factor $V_{transp}$ with fixed (FIXEDWT) and modelled (MODELWT) water table values. The plant transport clearly interacts with the water table model applied. For FIXEDWT, an increase in $CH_4$ flux occurs with increasing $V_{transp}$, for MODELWT a decrease.

the $CH_4$ flux. Both in the model and in real vegetated wetland ecosystems, the plant flux is the dominant flux (Walter and Heimann, 2000; Couwenberg, 2009). Since oxidation during plant transport is linearly related to the plant flux, this is an expected result. Likewise, increasing NPP ($P_{max}$ parameter) also results in a linear increment of the $CH_4$ flux (Table 4). $CH_4$ production relates linearly to the amount of available labile organic carbon substrate, of which the production is also related linearly to NPP in the model.

Because of the possible interactions between water table and plant transport outlined above, the experiments for $V_{transp}$ have been carried out using two different approaches for water table, FIXEDWT and MODELWT (see Sect. 3.4). Figure 3 displays the results for different values of $V_{transp}$ for both approaches. An increase of $V_{transp}$ does not result in large changes of the $CH_4$ flux. Again this is not unexpected, given the model structure. Although $V_{transp}$ is a multiplication factor in modelling the plant-mediated $CH_4$ flux, the flux is limited by the balance between $CH_4$ production and oxidation, and cannot be higher than the net production plus soil storage change. However, the interaction with the water table model causes opposing results. For FIXEDWT, the flux increases with rising $V_{transp}$, for MODELWT it decreases. In the model, the amount of plant-mediated transport is limited by the amount of roots below WT, which is exponentially distributed. With MODELWT, this produces a decrease of the flux at low WT, which is stronger at high values of $V_{transp}$; with FIXEDWT, this does not occur. Remarkably, the difference in behaviour of $V_{transp}$ with the water table model is very clear for the land areas and absent for the exposed seafloor areas.

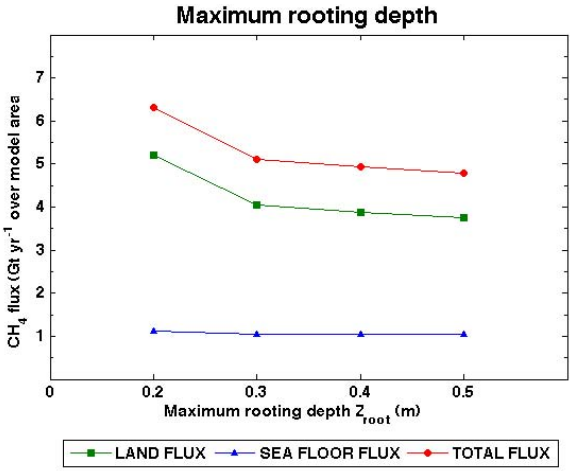


**Fig. 4.** Increasing the maximum depth of the vegetation root system results in a nonlinear decrease of the $CH_4$ fluxes.

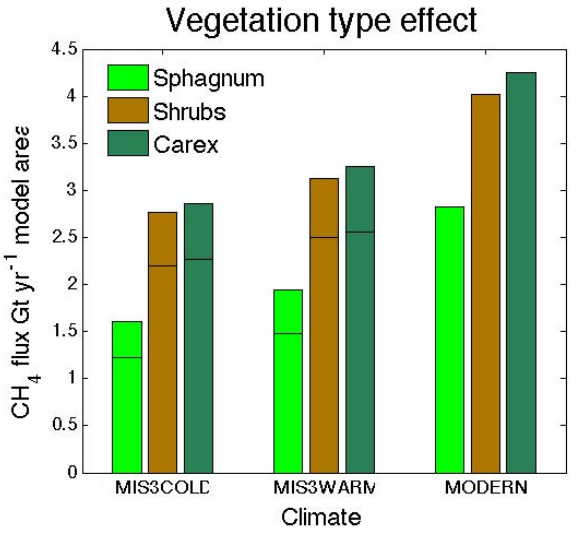


**Fig. 5.** Fluxes for the wetland vegetation types serving as wetlands vegetation end members, for three modelled climates: MIS3COLD (stadial), MIS3WARM (interstadial), and MODERN (present climate). The horizontal lines in the bars separate the land flux (below the line) and the exposed seafloor flux (above the line) for the MIS3 climates.

In Table 4 the effect of root exudation as a mass fraction of below-ground labile organic matter substrate for $CH_4$ production is listed. The fluxes increase slightly with higher value because of higher substrate availability for methanogens. However, the increase is less than 5 % for a threefold increase of $f_{ex}$. We tested here also for interaction with the water table model, because the water table also determines how much of the labile organic matter becomes available for $CH_4$ production. However, interaction with the water table model is minor, the increase of the $CH_4$ flux with $f_{ex}$ is slightly stronger with FIXEDWT, since the water table with MODELWT results in a lower water table for part of the year and less anaerobic decomposition of the exudates. For the exposed seafloor, the flux with FIXEDWT is slightly higher than that with MODELWT, which is opposite for the land area.

The maximum rooting depth $Z_{root}$ has a non-linear influence on the $CH_4$ emissions (Fig. 4). At a larger rooting depth, the flux decreases and this decline is strongest at shallow rooting depths. However, a rooting depth of 0.2 m is shallow for most wetland ecosystems with vascular plants and should be considered as a minimum. In the model, the amount of plant transport at a certain depth is the product of $V_{transp}$, the root density and the soil $CH_4$ concentration, which product is in turn is reduced by the oxidated fraction $f_{ox}$ (Walter and Heimann, 2000). This results in a larger total fraction of oxidized $CH_4$ with larger rooting depth, in accordance with the large role of rhizosphere oxidation discussed above.

The VEGETATION experiment highlights the range of emission values that can be expected assuming changes in (paleo)vegetation of the wetlands. To highlight the effect of each vegetation type, runs have been performed assuming that each of these vegetation types is the only one present (Fig. 5). Taking the *Sphagnum* type as reference, the *Carex* and Shrub types result in 50 % and 42 % higher fluxes for the MODERN experiment. For the MIS3COLD experiment, the increase is 77 % and 72 %; for the MIS3WARM experiment, the increase is 68 % and 61 %. If we then compare MIS3COLD (*Carex* type) and MODERN (*Sphagnum* type), the fluxes from the two climates hardly differ; the MS3COLD climate has even a slightly higher flux (2.9 vs. 2.8 Gt $CH_4$ $yr^{-1}$); the flux of MIS3WARM for the *Carex* type is conspicuously higher than MODERN with *Sphagnum*, 3.3 Gt $CH_4$ $yr^{-1}$).

## 5 Discussion

Model reconstructions are fundamental tools whenever proxy data are missing in paleoclimate research, but they are based on assumptions on model structure, parameters and model input. The PEATLAND-VU model is able to simulate the seasonal changes in $CH_4$ flux from a wide range of temperate and arctic wetland sites (van Huissteden et al., 2006; Petrescu et al., 2008; van Huissteden et al., 2009), at the level of individual sites. van Huissteden et al. (2009) have shown that the model is relatively insensitive to the soil definition, while it is strongly sensitive to vegetation parameters, in particular oxidation during plant-mediated transport.

The model contains simulation of the soil temperature, including soil freezing and active layer depth and the active layer thickness (Petrescu et al., 2008). Since peat and humic material are explicitly incorporated as organic C reservoirs (van Huissteden et al., 2004), the model can simulate C fluxes resulting from decomposition of old carbon in soils.

However, this results mostly in higher $CO_2$ fluxes, since old C reservoirs generally consist of refractory material that is not easily decomposed by methanogens. As mentioned in Sect. 3, a small contribution from decomposing peat is included for $CH_4$ formation by assuming a rate constant $R_{0,\mathrm{peat}}$ of $0.01 \times$ the $R_0$ for labile organic matter in the model. The low decomposition rate agrees well with the observations on organic matter in Pleistocene successions in northern Europe, which is generally well preserved (van Huissteden, 1990; Bos et al., 2001); therefore, large scale decomposition of older organic matter in sediments during rapid climate changes of the LG is unlikely. The thickness of the organic layer in the model soil profile definition (Sect. 3.4) also precludes large scale decomposition of old carbon. The $CH_4$ emissions modelled here are largely fluxes generated by decomposition of labile organic matter directly derived from ecosystem NPP.

The delineation of ice cover extent and exposed seafloor areas is also subject to large uncertainties. PEATLAND uses the climate output and boundary conditions from the STAGE 3 Project model. The rather small Scandinavian ice caps assumed in the STAGE 3 project are confirmed by recent data. According to Helmens et al. (2007), ice-free conditions occurred in northern Finland during MIS3 interstadials. The area of exposed seafloor is based on other models used as boundary conditions for the climate model (van Andel, 2002; Arnold et al., 2002). Our model does not account for permafrost degradation. During MIS3 interstadials, thaw lake formation may have occurred (van Huissteden, 1990; Ran et al., 1990; Bos et al., 2001). Nonetheless, our values are still consistent with those published by van Huissteden (2004) and in line with earlier estimates by Brook et al. (2000) based on inverse modelling.

Our model shows that vegetation characteristics are a large source of uncertainty. In particular, assumptions on the amount of $CH_4$ oxidation during plant-mediated transport ($f_{\mathrm{ox}}$) have a large effect on the results, but to a lesser extent also NPP, maximum rooting depth $Z_{\mathrm{root}}$ and transport parameter $V_{\mathrm{transp}}$. Higher $f_{\mathrm{ox}}$ gives a strong decrease of the $CH_4$ fluxes. The production of labile organic matter in the root zone $f_{\mathrm{ex}}$ had only a very minor effect. Larger $Z_{\mathrm{root}}$ results in decreasing flux. It influences the emissions from vegetation because of its interaction with $V_{\mathrm{transp}}$ and $f_{\mathrm{ox}}$; a larger rooting depth supports more oxidation, which agrees with experimental observations (Smialek et al., 2006). Clearly, oxidation of $CH_4$ in vegetation is a highly important parameter determining the wetland $CH_4$ flux. Changes in the vegetation characteristics that affect oxidation therefore potentially affect $CH_4$ fluxes more strongly than changes in climate affecting water table or soil temperatures. In Fig. 2, a change in $f_{\mathrm{ox}}$ from 0.2 to 0.9 results in an 58 % decrease of the $CH_4$ flux, while in Fig. 5 the flux decrease between MODERN and ST3COLD climate ranges between 31 and 43 %.

The transport parameter $V_{\mathrm{transp}}$ clearly interacts with the water table input of the model. When a fixed water level is imposed, the fluxes change in both magnitude and trend. This interaction is driven by the effect of the exponential root distribution in the model on the plant mediated transport. Also for $f_{\mathrm{ex}}$ a slight interaction is noted, resulting in a stronger increase of the flux with increasing $f_{\mathrm{ex}}$ with FIXEDWT. However, compared to the effect of oxidation, these interaction effects are of minor significance.

Exposed seafloor areas not only contribute to the MIS3 $CH_4$ fluxes, they also interact with some of the vegetation parameters and the water table model, notably for $V_{\mathrm{transp}}$. $V_{\mathrm{transp}}$ interacts strongly with the water table model for the land areas but not for the seafloor areas. An explanation for this interaction is the difference in elevation distribution between the land areas and the exposed seafloor areas. The latter have a much smaller range in elevation. The climate model grid cells are small enough to resolve regional relief in Europe and the model can therefore simulate the effects of topography on regional climate. The resulting regional differences in precipitation and temperature in turn affect the modelled water table in the MODELWT experiments (not in FIXEDWT which assumes a constant water table at the surface throughout the year). Consequently, the difference in elevation distributions of land and seafloor areas also affect vegetation parameters that strongly interact with the water table and with the way it is modelled. For the exposed seafloor areas, this results in a much smaller spatial variability of the water table. This is combined with a weaker seasonality of the precipitation distribution in generally maritime climate conditions, resulting also in less temporal variability of the water table; hence, the MODELWT water tables will also be more constant and similar to FIXEDWT. However, since the exposed seafloor areas are small relative to land area, this has only a minor effect on the total flux.

Interaction between the vegetation parameters are difficult to test in our modelling setup, because the number of model runs to be performed increases rapidly with the number of parameters. Van Huissteden et al. (2009) tested the PEATLAND-VU model on the scale of observation sites using monte-carlo methods. This showed the presence of interaction between $f_{ox}$, $V_{\mathrm{transp}}$ and microbial $CH_4$ production rate $R_0$; a higher $V_{\mathrm{transp}}$ and $R_0$ can for instance compensate for a higher $f_{\mathrm{ox}}$.

In the case of paleo-wetland fluxes, vegetation parameters need to agree with paleobotanical reconstructions. However, species cover percentages are difficult to derive from paleobotanical data (e.g. Huntley et al., 2003). Moreover, wetland vegetation tends to have a mosaic-like pattern. Ran (1990) could determine vegetation communities based on detailed macro-remain analysis. Her MIS3 stadial and interstadial wetland vegetation in the eastern Netherlands consisted of a pattern of treeless vegetation communities dominated by *Cyperaceae* and *Juncaceae*, with varying amounts of non-*Sphagnum* bryophytes and a water table generally close to or above the soil surface. Carex roots dominated the organic matter of the silt and peat beds deposited in these wetlands.

Areal percentages of vegetation communities could not be determined, however. By comparison, a present-day Siberian tundra site consist of a mosaic of vegetation dominated by either *Carex* species (or *Sphagnum* in the parts with high water table, and *Betula nana* or *Eriophorum* tussocks in the drier parts. The Carex-dominated areas occupy up to 20 % of the area, Sphagnum-dominated vegetation up to 45 %, drier vegetation types vary between 35 and 90 % (van der Molen et al., 2007).

The *Sphagnum* mosses are important in the present-day $CH_4$ cycle, but their contribution may have been much smaller in glacial paleo-climates as is shown by the paleobotanical record. Conversely, *Carex* spp. and graminoid vegetation in general provide the most effective pathway to transport $CH_4$ from soil into the atmosphere (Hornibrook, 2009). Low transport, high oxidation vegetation (*Sphagnum*-type) produces much lower fluxes than high transport rate, low oxidation vegetation (*Carex*-type), with Shrubs intermediate as summarized in Fig. 5.

Our model shows that for the colder glacial climates, the dominance of *Carex*-type vegetations may have resulted in $CH_4$ fluxes of similar or even higher magnitude, as those for the modern climate with largely *Sphagnum*-dominated vegetation in wetlands, despite the colder climate which should have reduced methanogenesis. Of course, we used end members for the wetland vegetation in our model experiments which exacerbates the differences, and in present-day wetlands large areas are covered with *Carex*-type vegetation as well. Nonetheless, it indicates that glacial wetland $CH_4$ fluxes should have been relatively high compared with those of present-day wetlands because of the differences in vegetation-related oxidation and transport of $CH_4$.

In present-day northern wetland environments, thawing permafrost or an increase of the active layer thickness is often accompanied by a change from a *Sphagnum* -dominated vegetation towards a vegetation cover with predominant *Carex* and *Eriophorum spp.*, leading to increased $CH_4$ emissions (Christensen et al., 2004; van Huissteden et al., 2005). Our results show that such an increase in *Carex*-dominated wetland ecosystems may result in a considerable rise of $CH_4$ fluxes, although this may also be compensated by a larger rate of $CO_2$ uptake (Turetsky et al., 2007). Conversely, for the early Holocene, the decreasing trend of $CH_4$ (EPICA members, 2004; Ruddiman, 2007) may also be caused by the gradual expansion of Sphagnum-dominated wetlands at the expense of other wetland types.

## 6 Conclusions

The emissions of $CH_4$ from wetland soils to the atmosphere are not only a matter of hydrology and wetland area, but also depend on a more complicated balance between all the sinks and sources of $CH_4$ within the soil-vegetation-atmosphere continuum, including all methanotrophic and methanogenic bacteria involved in such reactions. Our model experiments show that in Pleistocene climates $CH_4$, fluxes are sensitive to wetland vegetation characteristics: oxidation during soil-vegetation-atmosphere exchange, NPP, rooting depth and plant-mediated transport rate. Oxidation proves to be a major parameter which effectively modifies fluxes.

Particularly, flux differences between *Carex*-dominated and *Sphagnum*-dominated wetlands may be large, 50 % to 78 % relative to *Sphagnum*. We have shown that vegetation characteristics cannot be neglected when paleo-wetland fluxes are modelled, and therefore paleobotanical information is crucial to estimate past $CH_4$ emissions. Our experiments show that changes in wetland vegetation may alter $CH_4$ fluxes drastically. This pertains to past Pleistocene as well as future Anthropocene wetland $CH_4$ fluxes. Because of differences in vegetation derived from the paleobotanical record, the glacial wetlands in Europe may have had similar or even higher fluxes than the present-day wetlands.

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